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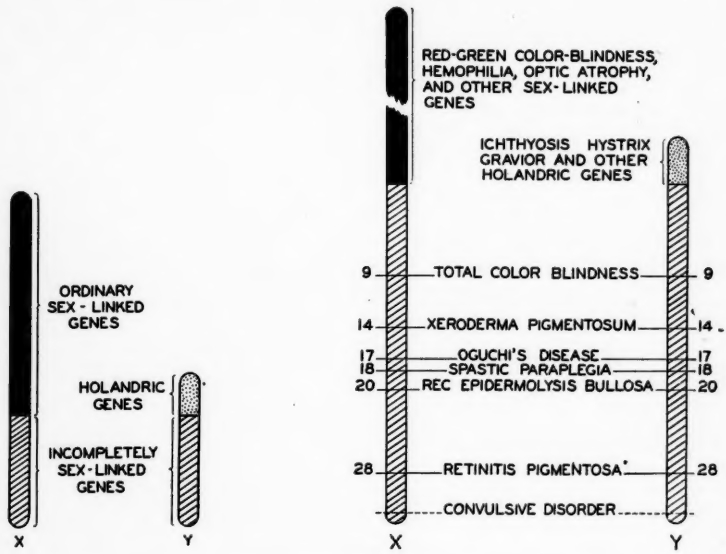

A LINKAGE MAP OF HUMAN SEX-CHROMOSOMES

(SEE PAGE 207)

Teosinte in Mexico

Wheat × Rye-Grass Hybrids

Species Hybrids in the Tomato

Wingless Chicks—A New Lethal

Knobs and Chromocenters in Maize Chromosomes

VOLUME 34 JULY, 1943 NUMBER 7

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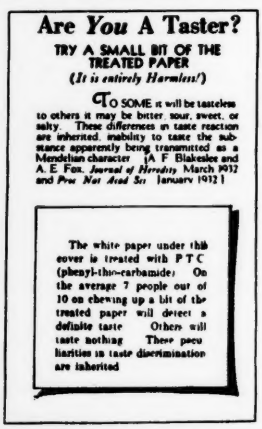
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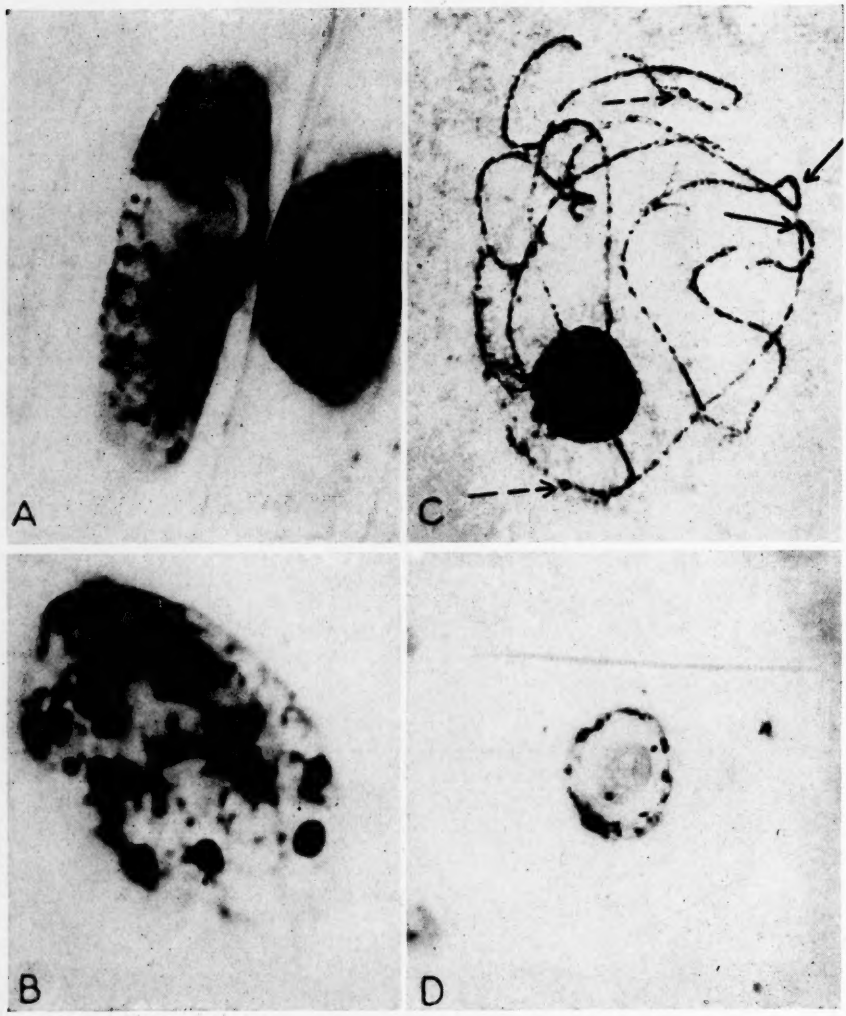

KNOBLESS AND KNOBBED MAIZE CHROMOSOMES

Figure 1

A—Interkinetic nucleus of line *E*, which had no conspicuous knobs in the pachytene chromosomes and was free from *B* chromosomes; stained with Fuelgen reaction. This nucleus has no large, conspicuous chromocenters. The Fuelgen-negative nucleolus is clearly visible. Approximately × 3200. *B*—Interkinetic nucleus of line *A*, which had a total of nine knobs on the pachytene chromosomes, showing large distinct chromocenters formed by the knobs. Stained with Fuelgen reaction. Approximately × 3200. *C*—Pachytene of line *C* stained with acetocarmine. Two knob-bearing chromosomes are indicated by broken arrows, while the deeply staining regions adjacent to the centromeres are indicated by solid arrows. The nucleolar organizer on chromosome 6 is not visible in this preparation. × 800. *D*—Transverse section of an interkinetic nucleus of maize showing its vesicular nature. A single nucleolus is present which occupies a central position in the nucleus. The two nucleolar organizers are the deeply staining bodies adjacent to the nucleolus. Fuelgen. × 1200.

THE FORMATION OF CHROMOCENTERS IN INTERKINETIC NUCLEI OF MAIZE BY KNOBS AND *B* CHROMOSOMES

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TWO different types of chromatin, heterochromatin and euchromatin, are present in the chromosomes of plants and animals. Heterochromatin is heavily charged with thymonucleic acid at prophase and interkinesis and consequently is heteropycnotic or deeply staining at those stages. Euchromatin has been shown by the Feulgen reaction and by ultra-violet absorption to be less heavily charged with thymonucleic acid and is genetically active in contrast to the apparent genetic inertness of heterochromatin. Darlington and La Cour[1,2] have shown that temperatures of 3°C and lower inhibit the formation of thymonucleic acid in the nuclei of *Paris polyphylla, Trillium* sp. and *Fritillaria pudica.* At these low temperatures the normal staining reaction of euchromatin and heterochromatin is reversed, the euchromatic regions staining deeply with Feulgen while the heterochromatic regions stain lightly. However, in general those structures staining relatively more intensely with the Feulgen reaction may be described as heterochromatic.

The pachytene chromosomes of maize are of two kinds, classified as *A* chromosomes and *B* chromosomes. The *A* chromosomes, stained with aceto-carmine or the Feulgen reaction after acid-alcohol fixation, have four classes of deeply staining elements: knobs, chromomeres, the nucleolar organizing region of chromosome 6, and the intensely staining regions adjacent to the centromere in several of the chromosomes (see Figure 1*C*). The knobs are discrete areas of heterochromatic material, each knob being constant in size, number and position in a given inbred genetic strain. Knobs on non-homologous chromosomes are often fused at pachytene, but this fusion does not persist in later prophase stages. This fusion may indicate that the material constituting the different knobs lacks specificity—i.e., that the different knobs are composed of the same substance. Knobs are typically heterochromatic in their staining reaction and genetic activity, since they stain intensely and are apparently genetically inert. Knob number varies from strain to strain, and knobless maize strains have been reported by Longley[6] and Mangelsdorf and Reeves.[7] Chromomeres are small, discrete, intensely staining particles invariably present in the pachytene chromosomes of maize. They are considerably smaller and far more numerous than the knobs. A qualitative as well as a quantitative difference between knobs and chromomeres probably exists, since chromomeres do not fuse with one another, and their number is probably constant from strain to strain. All but the smallest of knobs are much larger than chromomeres. The nucleolar organizing region may be readily distinguished from knobs by its position in chromosome 6 adjacent to the nucleolus and by its reticulate appearance.[10] The deeply staining regions adjacent to the centromere in several of the pachytene chromosomes of maize are distinguishable by their characteristic position and their diffuse appearance in contrast to the smooth, glossy appearance of knobs.

Certain strains of maize have, in ad-

*The author wishes to express his appreciation to Professor M. M. Rhoades for aid and advice during the course of this investigation and to Professor P. C. Mangelsdorf for generously furnishing the strains of Peruvian maize.

dition to the *A* type chromosomes, varying numbers of *B* type chromosomes. The *B* chromosomes are largely heterochromatic and stain intensely at pachytene. Their presence in low numbers has no apparent effect on the phenotype of the plant. However, ten or more *B* chromosomes in a single plant bring about a gradual reduction in fertility, and higher numbers of *B* chromosomes cause other deleterious effects.[11]

In order to determine if *B* chromosomes and the intensely staining elements of the pachytene chromosomes are evident in the interkinetic nuclei, root tip smears and sections of four different lines of maize were stained by the Feulgen reaction after fixation in Craf fluid. The microsporocytes for pachytene analysis were stained either with acetocarmine or the Feulgen reaction after acid alcohol fixation. The comparison of structures in the meiotic chromosomes and in somatic nuclei is justifiable, since the meiotic chromatid which becomes the chromosome of the microspore passes, after fertilization, through innumerable mitotic divisions during development and emerges unaltered at the prophase of meiosis at sexual maturity of the plant. The microsporocytes stained by the Feulgen reaction corroborated the analysis made from acetocarmine smears. The deeply staining elements of the pachytene chromosomes were heavily charged with thymonucleic acid since the Feulgen reaction is specific for that substance. The nucleolus, which is devoid of thymonucleic acid, did not stain with the Feulgen reaction but stained deeply with acetocarmine.

Sections of root tip tissue directly back of the meristematic region showed the interkinetic nuclei of maize to be vesicular according to the classification of Manton.[8] The two nucleoli were generally fused in the center of the nucleus with the nucleolar organizers adjacent to the fused nucleolus. The chromatic material, excepting the nucleolar organizers, was distributed around the periphery of the nucleus (Figure 1*D*). Deeply staining, discrete masses of heterochromatin (chromocenters) and more diffuse areas of heterochromatin were evident in the nucleus (Figure 1*A* and *B*). The varying number of sharply delimited chromocenters in different strains of maize having different numbers of knobs suggested a possible relationship between the well defined knobs of the pachytene chromosomes and the chromocenters of interkinetic nuclei. The diffuse areas of heterochromatin in the interkinetic nuclei may be related to the deeply staining regions adjacent to the centromere in several of the pachytene chromosomes. The chromatic bodies of interkinetic nuclei have been designated by the terms "chromocenter" (Heitz[4,5]), and "prochromosome" (Rosenberg[12]). In this study the term chromocenter is preferred to prochromosome, since the latter term indicates a correlation of heteropycnotic bodies in the interkinetic nucleus to chromosome number, while the former term as used by Heitz indicates the correlation of heteropycnotic bodies in the interkinetic nucleus to specific chromosomal parts. Counts of knob and chromocenter frequencies were made in several strains to determine if a correlation exists between knobs and chromocenter number. Chromocenter counts were made prior to knob counts to eliminate the possibility of observational bias in the data. These data are presented in Table I.

These data show a good correlation between mean chromocenter number and knob number. A knob number of nine means that a total of nine knobs was present at pachytene. If both members of a pair of chromosomes (chromosome 7, for example) had a knob, this would count as two knobs, since each chromosome bore one. The range, and the fact that mean chromocenter number was less than the value for knob number, indicate that some fusion of chromocenters occurred. That fusion occurs is also suggested by the fact that certain of the chromocenters appeared incompletely fused and some of the chromocenters were conspicuously larger in those nuclei where the chromocenter number was less than the mean. The occasional occurrence of nuclei with chromocenter

numbers higher than knob numbers may be due to fusion of small knobs which are difficult to distinguish from large chromomeres at pachytene and to the misclassification of dense aggregates of diffuse heterochromatin as chromocenters.

The knobs of line *C* were relatively uniform in size, and the chromocenters were approximately uniform in size excepting the nuclei where fusion of chromocenters occurred. Two of the knobs of line *B* were considerably larger than the other knobs of the complement, and correspondingly one or two of the chromocenters were consistently larger than the others. This indicates that large knobs give rise to large chromocenters and small knobs to small chromocenters.

The interkinetic nuclei of stylar tissue (silks) of line *A*, stained by the Feulgen reaction, were examined to determine if chromocenter number varied significantly in different somatic tissues. Comparison with the data obtained from the examination of the interkinetic nuclei of the root tips of the same plant shows no significant difference.

Interkinetic nuclei of line *D*, which was free from knobs but had four *B* type chromosomes with the same architecture as that described by McClintock,[9] were examined for chromocenters. The modal class, 4.00, and the mean number of chromocenters, 3.27, indicate a correlation of chromocenter number and *B* chromosome number. The chromocenters from *B* chromosomes were not visibly different from the chromocenters resulting from the knobs of the other lines examined. *B* chromosomes are much larger than knobs, but no corresponding size difference in the chromocenters was evident. This suggests that all the heterochromatin of the *B* chromosomes may not be involved in the formation of chromocenters. *B* chromosomes have four distinct pycnotic or deeply staining regions at pachytene. The pycnotic region adjacent to the terminal or slightly subterminal centromere appears more discrete than the other heteropycnotic regions, which are relatively diffuse by comparison. This pycnotic region proximal to the centromere more closely resembles the knobs

TABLE I. Knob and B Chromosomes of Five Strains of Maize.

Tissue	Line	Knob number	B chromosome no.	No. of nuclei	Mean chromocenter no.	Range	Modal class
Root	(genetic stock) A	9	0	100	8.16	4-11	8.00
Style	(genetic stock) A	9	0	100	8.00	4-12	8.00
Root	(inbred line) B	6	0	100	5.05	2-8	5.00
Root	(inbred line) C	6	0	100	5.22	2-6	5.00
Root	(Peruvian maize) D	0	4	100	3.27	1-5	4.00
Root	(Peruvian maize) E	0*	0	100	0.22	0-1	0.00

*This strain of maize of Peruvian origin was believed to be knobless. However, examination at pachytene showed that a small knob, hardly larger than some chromosomes, was present on chromosome 7. It is extremely likely that the occasional small chromocenters observed in the interkinetic nuclei are due to this small knob.

of the *A* type chromosomes in size and appearance than do any of the other regions. Consequently the pycnotic region adjacent to the centromere probably gives rise to the chromocenters, while the other deeply staining regions probably go to form the diffuse heterochromatin of the interkinetic nuclei.

Line *E* came from a Peruvian strain believed to be knobless. It had no large knobs and was also free from *B* chromosomes. However, it was homozygous for a small knob on chromosome 7. This knob is in a different size-category from the large distinct knobs present in the other examined lines. Seventy-eight of the 100 nuclei examined were entirely free from chromocenters with the exception of the two nucleolar organizers which are necessarily present in every nucleus. Twenty-two nuclei were scored as having a single small chromocenter which undoubtedly was related to the small knob present on the chromosome 7 (Figure 1*A*). It seems reasonable to conclude that both the number of *B* chromosomes and the number of knobs determine the number of chromocenters occurring in the interkinetic nuclei.

Summary

Resting nuclei of maize stained with Feulgen contain discrete, deeply-staining bodies in addition to diffuse chromatic material. These deeply-staining bodies are called chromocenters. A good correlation was found between the number of chromocenters in the interkinetic nuclei and the number of knobs present in the pachytene chromosomes.

In strains free from conspicuous knobs but possessing *B* chromosomes a good correlation was also found between the number of *B* chromosomes and the number of chromocenters. The chromocenters derived from *B* chromosomes are not so large as those from some of the larger knobs, which indicates that all of the heteropycnotic material observed in the *B* chromosomes at pachytene is not represented in the chromocenter. That portion of the *B* chromosome immediately adjacent to the centromere of the *B* chromosome is more knob-like in appearance than other portions of the chromosome, and it is believed that it is this proximal portion which forms the chromocenter.

Plants free from conspicuous knobs and *B* chromosomes have a great majority of their interkinetic nuclei free from many structures which might be interpreted as chromocenters (except for the two nucleolar organizer regions on chromosome 6). That chromocenters often fuse is indicated by the range in number and size. Strains with knobs of approximately uniform size have chromocenters of uniform size—barring fusion—while strains with different sized knobs have a marked range in size of chromocenters.

Occasionally the number of bodies classified as chromocenters was greater than the number of conspicuous knobs. This may have been due to the misclassification of diffuse heterochromatin as chromocenters or more likely to the failure to distinguish small knobs at pachytene. Fusion of two or more of these small knobs might give rise to recognizable chromocenters.

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HYBRIDS OF THE CHILEAN TOMATO

Sterile and Fertile Plants of *Lycopersicon Peruvianum* var. *Dentatum* Dun. (*L. Chilense* Dun.) and Diploid and Tetraploid Hybrids With Cultivated Tomatoes*

MARGARET MANN LESLEY AND J. W. LESLEY
University of California Citrus Experiment Station

HOLMES[5] has pointed out the possible value of *Lycopersicon peruvianum* var. *dentatum* (*L. chilense*) as a source of disease resistance and has succeeded in crossing it with the cultivated tomato. Recently, a strong tendency to escape infection with tobacco mosaic has been found in derivatives of this cross.[6] No adequate resistance to curly top, a serious disease of tomatoes in the western United States, has been found in any cultivated tomato or near relative, in spite of attempts by several investigators. The variety *dentatum* has, however, been found by Virgin[10] to be resistant to this disease, and this finding has been confirmed by Dr. H. L. Blood, Plant Pathologist, U. S. Department of Agriculture, and by the junior author. The present data were obtained in an investigation of the sterility encountered in attempting to breed a curly-top-resistant variety of tomato by crossing *dentatum* with cultivated varieties.

Lycopersicon peruvianum var. *dentatum*, also known as the Chilean tomato, is placed by Muller,[8] in the subgenus *Eriopersicon*. All cultivated tomatoes are in the subgenus *Eulycopersicon* and either belong in the cultigen *L. esculentum* or are hybrids of *L. esculentum* and *L. pimpinellifolium*. *L. peruvianum* and its variety *dentatum* have narrower cotyledons, smaller leaves, and more slender and brittle stems than *L. pimpinellifolium* or *L. esculentum*. They are also canescent, owing to an abundance of short trichomes and a paucity of glandular hairs, and usually have pseudostipules on the stem, and bracts on the inflorescence. The style and staminal column are usually much bent. The fruit of *L. peruvianum* and of *dentatum* is pubescent and, when ripe, greenish white often tinged with purple. Dark-green or purple sectors may be present on the surface, especially at the basal end. The seeds are naked except at the apex.

According to Muller,[8] *dentatum* (*L. peruvianum* var. *dentatum*) is extremely variable. A few individuals occur which are clearly intermediate between it and the typical form of the species, *L. peruvianum*. *Dentatum* is generally more canescent and pilose and has more capitately stellate hairs than *L. peruvianum*; the leaf is broader and more fernlike, more deeply dissected and often partially bipinnate, and the leaflets tend to be more acute. The fruit usually contains fewer seeds than that of *L. peruvianum*.

At Princeton, New Jersey, and at Davis, California, *dentatum* has been difficult to propagate. At Riverside, California, also, the plants were slow-growing and subject to insect injury. They bloomed sparingly and only at intervals and were distinctly unfruitful. The shoots were brittle, subject to decay, and not easily induced to root.

A Sticky-Chromosome Type of *Lycopersicon peruvianum* var. *dentatum*

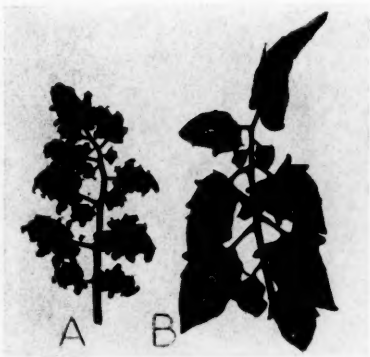
Three closely similar seedlings, 41.-096.1, 39.063.2, and 41.039.1 (Figure 2*A*, *B*, and *C*), grown at Riverside, California, conformed to Muller's[8] description of *dentatum*. They were all descended from Holmes's[5] original plant of *L. chilense* Dun. and conform to his description of it. This plant came from seed from a thirteen-year-old herbarium specimen of a wild plant collected by I. M. Johnston in Chile. At Riverside,

*Paper No. 487, University of California Citrus Experiment Station, Riverside, California.

STICKY-CHROMOSOME CHILEAN TOMATO PLANTS COMPARED WITH NORMAL

Figure 2

A and *B* are parts of two plants of *dentatum* having sticky chromosomes, compared with a fertile plant having normal chromosomes (*C*). All of these plants arose as second generation seedlings from a single *dentatum* seed which had been stored for many years. The "sticky" characteristic appears to be a gene mutation, though this could not be proved conclusively because of the complete sterility of the sticky plants.



TRIPLOID LEAVES

Figure 3

Forty-five seedlings from an F_2 plant of an *esculentum* × *dentatum* hybrid were apparently all triploids. They varied considerably in appearance but resembled *dentatum* more than they did *esculentum*. Fruits were produced late in the season and were seedless.

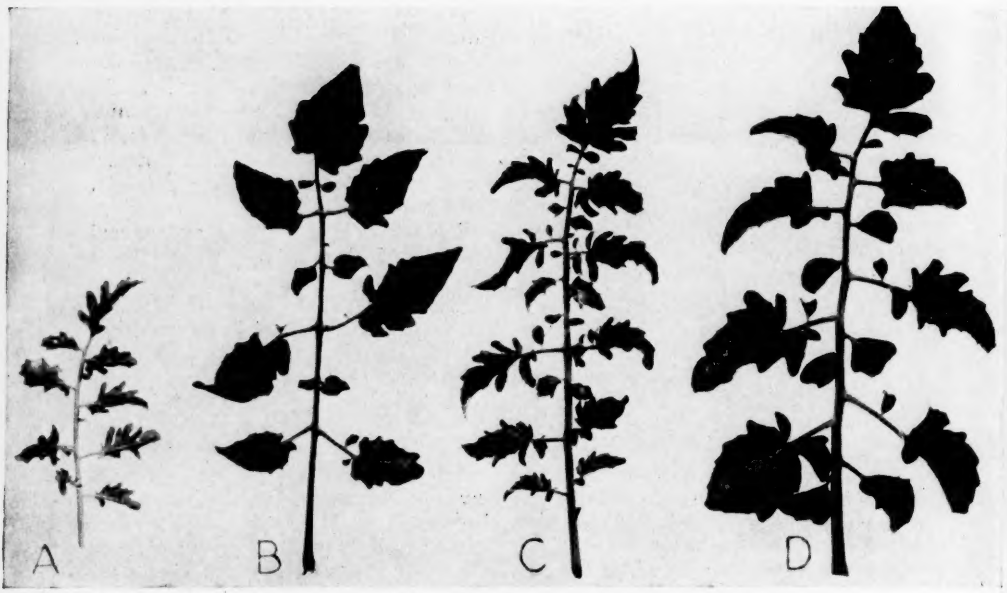
39.063.2 was the slowest growing, had the smallest leaves, bloomed the most sparingly, and had no purple color in the buds or stem. The anthers of 41.096.1 were slightly less connate than the others. Plants 39.063.2 and 41.096.1 had very little pollen and were sterile, setting no seeds from either selfing or crossing with cultivated tomatoes. Plant 41.039.1 was fertile when selfed or crossed, as pollen parent, with cultivated tomatoes.

All three *dentatum* plants have been propagated by cuttings, and the resulting clones have been grown in both field and greenhouse. In both environments meiosis in 39.063.2 and 41.096.1 was like that described by Beadle[1] for the sticky-chromosome plants of maize. The nuclear wall of the pollen mother cell usually disappears while the chromosomes are still greatly elongated and closely entangled. It seems probable that very few such pollen mother cells ever complete the meiotic divisions. In a very few cells, counts of 12 very elongated pairs of chromosomes can be made. Contraction is somewhat variable, but the pairs of chromosomes are always more elongated than in cultivated tomatoes (Figure 5*A, B*). From one to six pairs often lie at right angles to the spindle (Figure 5*C, D*), as if the spindle fibers failed to function normally. At first anaphase, many of the chromosomes stick together and streams of chromatin connect the portions which eventually arrive at the poles (Figure 5*E, F*). Fragmentation and chromosome elimination are frequent at first and second telophase, and as many as six bits of chromatin may remain at the equator of each spindle. Very few normal-looking tetrads are formed, and the pollen is usually shrunken and abnormal. The chromosomes in young pollen are very variable, both in number and in size (Figure 5*G, H*). The differences in size shown in Figure 5*G* indicate that some whole chromosomes may pass undivided into the pollen. No study has been made of meiosis in the embryo-sac mother cells, but the sterility of these plants, both when selfed and when pollinated with cultivated tomatoes, indicates that these cells are abnormal also.

Since sticky chromosomes in maize, a similar condition, has been shown to be a simple Mendelian recessive,[1] and since two types of *dentatum*, fertile and sterile, have segregated out, it seems probable that sticky chromosomes in *dentatum* are due to a gene mutation. Beadle[2] states that in *Zea mays* "the chromosome behavior during mitosis and meiosis is strikingly similar to that observed in cells following X-ray treatment."

In *Datura*,[3] aging, with consequent drying of seed, appears to be associated with an increased mutation rate. All the *dentatum* plants grown in the present studies originated from a single aged seed.

Darlington[4] has reported that controlled starvation induces chromosome stickiness. This, he suggests, may be due to a supercharging of the chromosomes with nucleic acid. In the absence of genetic data, which it has not been possible to obtain because of the complete sterility of the sticky-chromosome *dentatum* plants, it seems probable that the stickiness may have resulted from injury to the stored food materials in the



LEAVES OF TOMATO SPECIES AND HYBRIDS

Figure 4

A—Leaf of *L. peruvianum* variety *dentatum*. *B*—Leaf of an F_1 plant of *L. esculentum* × *L. pimpinellifolium*. *C*—Diploid F_1 of a triple hybrid (*L. esculentum* × *L. pimpinellifolium*) × *L. peruvianum* variety *dentatum*. *D*—Tetraploid F_1 sibling of the diploid shown in *C*. The tetraploids are darker green, have larger leaves and flowers than the diploid hybrids and are even less fruitful. Pairing between the chromosomes of the two species indicates that they are more closely related than one would suspect on account of great differences in appearances.

seed, which caused a starved condition in the young plant.

Dentatum plant 41.039.1 produced a fair amount of pollen but only very few fruits from natural pollination in the field. In the greenhouse in winter, it produced more pollen and was fairly self-fertile. Numerous viable seeds were obtained when its pollen was applied to the stigmas of cultivated tomatoes.

Pollen mother cells of plant 41.039.1 have 12 dumb-bell-shaped pairs of chromosomes in diakinesis and first metaphase, very much like those of the tomato. Meiosis is usually normal, but in very hot weather a great majority of the chromosomes are unpaired at diakinesis, and more or less complete nonreduction occurs, as a result, in as many as half the pollen mother cells (Figure 6*A-C*). Under cultivation at Riverside, California, it would seem that even 41.039.1, which is the most nearly normal of the three *dentatum* plants, is so unstable that it would not be expected to perpetuate itself under natural conditions.

Although nonreduction also occurs in cultivated tomatoes in hot weather, it is far less frequent than in *dentatum* and results from spindle failure early in first anaphase, followed by incorporation of all 24 single chromosomes into one metaphase plate, and not, so far as has been observed, from a failure of conjugation, as in *dentatum*.

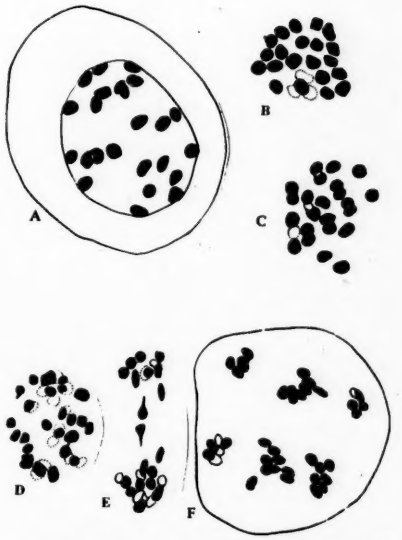
Diploid and Tetraploid F_1 Hybrids

One plant of *L. esculentum*, 41.082.1, and two F_1 hybrids of *esculentum* × *pimpinellifolium*, 41.080.1 and 41.086.1 (Figure 4*B*), as seed parents, were crossed with *dentatum* plant 41.039.1.

MEIOTIC DETAILS OF "STICKY" CHROMOSOMES

Figure 5

Details of meiosis in plant 41.096.1, of *L. Peruvianum* var. *dentatum*. This plant was sterile and the cytological examination showed the chromosomes to be "sticky," resembling a similar situation described by Beadle in maize. *A* and *B*—Elongation of the chromosomes at diakinesis. *C* and *D*—Extreme elongation at first metaphase; *C* shows three pairs, *D* two pairs, more or less at right angles to their normal alignment at first metaphase. A portion of one chromosome is connected to the main body by slender strands in *B* and *C*. *E*—Slender strands of chromatin which usually connect the two groups of chromosomes at first anaphase. *F*—A slightly later stage with six bits of chromatin lagging. *G* and *H*—Young pollen grains showing variability in number and size of chromosomes.



NORMAL MEIOSIS IN *DENTATUM*

Figure 6

Meiotic figures in plant 41.039.1, a fertile plant of *L. Peruvianum* var. *dentatum* with non-sticky chromosomes, during hot weather. In *A* only one pair of chromosomes is present at diakinesis; in *B* no pairs are present; in *C* seven pairs. *D*—Mixture of division of univalents and reduction commonly seen at first anaphase. *E*—Lagging and dividing chromosomes at first anaphase. *F*—Many laggards at second telophase.

Of 152 seeds from 41.080.1 and 41.086.1 as seed parents, 82 germinated, but of those from the *esculentum* seed parent, only four out of 32 grew.

All these F_1 hybrids of cultivated tomatoes and *dentatum*, like those described by Holmes,[5] were extremely vigorous, bloomed profusely, and produced a fair amount of pollen. They were distinctly unfruitful and partially sterile, but in the field at Riverside toward the end of the season the F_1 (*esculentum* × *pimpinellifolium*) × *dentatum* hybrids especially, produced a fair number of fruits and seeds. Pollen from several F_1 plants applied to tomato stigmas produced viable seeds.

The more conspicuous characteristics of *dentatum* (Figure 2*A*, *B* and *C*), in particular the canescence of the stem and leaves, the shape of the leaves, the presence of pseudostipules and bracts, and the pubescence of the fruit, were partially dominant. No dark-green or purple sectors were seen on the fruit, and the density of glandular hairs on the inflorescence and leaves also resembled that of the tomato parents.

The size of the fruit was nearer that of *dentatum* and rather suggestive of the geometric mean of the parent sizes, as reported by MacArthur and Butler[7] in tomato hybrids. The cultivated-tomato parents were *YYRR*, *Y* being the nor-

mal allele for yellow skin color and *R* for red flesh color of fruit. The skin of the ripe fruit of the F_1 hybrids was pale yellow and in this respect intermediate between the parental types. Evidently *dentatum* contains a gene or genes for non-yellow skin color other than *y*, which in cultivated varieties, is almost completely recessive to *Y*. The flesh color of *dentatum* is greenish white. The flesh color of the fruit of F_1 plants, when nearly ripe, was "ochraceous-buff," or about 15′*b* in the notation of Ridgway,[9] changing very slowly to a tone slightly deeper than "apricot buff" (11′*b*)[9] when overripe.

A preliminary pigment analysis of the ripe fruit by Dr. L. Zechmeister, of the California Institute of Technology, indicated that the greater part of the pigments consisted of carotenes, particularly β-carotene and an unidentified pigment with the α-carotene spectrum, and that only a small amount of lycopene was present. The apparent similarity in color to the Tangerine variety of tomato was deceptive, as prolycopene[11] was not present. Apparently *dentatum* has contributed to the F_1 plant a gene, or genes, not present in cultivated tomatoes, allelic and dominant to *R*, the major gene for lycopene formation, or nonallelic to *R* and suppressing its action .

In flavor, the fruit of the F_1 plants was distinctly sweeter than that of most cultivated tomatoes. Individual plants of the same F_1 family differed somewhat, especially in leaf shape and fruitfulness. This may have been due to the fact that all the cultivated tomatoes used as parents were heterozygous, especially, of course, the two *esculentum* × *pimpinellifolium* F_1 plants.

A tetraploid occurred in each of two families of four and 20 F_1 plants, from *esculentum* ♀ and *esculentum* × *pimpinellifolium* F_1 ♀, respectively, crossed with *dentatum* 41.039.1. Compared with their diploid sibs, the tetraploids were darker green, had larger leaves and flowers and thicker stems (Figure 4*C, D*), and were even less fruitful. Very late in the season they produced some fruits and a fair number of well-developed seeds. The *esculentum* × *dentatum* tetraploid was less fruitful than the (*esculentum* × *pimpinellifolium*) × *dentatum* tetraploid plant.

The pollen mother cells of the diploid F_1 species hybrids contained 12 pairs of chromosomes, and meiosis was similar in every respect to that in *L. esculentum*, except that in the F_1 extra microspores appeared to occur rather more frequently in hot weather. Quadrivalent formation in the tetraploid plants was similar to that in a tetraploid from *esculentum* growing in the field and examined at the same time; from three to nine quadrivalents were observed in each case.

Since the tetraploids contain the diploid chromosome complement of both species, one must assume that the chromosomes of the cultivated species and of *dentatum* are similar to the extent that preferential pairing occurs only exceptionally, if at all. The evidence indicates an unexpected genetic similarity of the chromosomes of the cultivated species and *dentatum*. The parent species *dentatum* and the cultivated species are so distinct that Muller[8] was led to place them in different subgenera. Moreover, no successful crosses of other races of *L. peruvianum* with cultivated tomatoes appear to have been reported. Comparison of phenotypes in this genus evidently gives unreliable evidence of crossability.

From open pollination of an F_2 plant of *esculentum* × *dentatum*, 48 seeds, kindly supplied by Dr. F. O. Holmes, of the Rockefeller Institute for Medical Research, Princeton, New Jersey, yielded a family of 45 plants. These plants varied considerably, especially in size, but all resembled dentatum much more closely than *esculentum*. Like *dentatum*, they were distinctly canescent and had stipules, bracts, and much-dissected leaves but were less variable than was to be expected in F_3 of a species cross (Figure 3*A, B*). They were extremely vigorous and floriferous, but were unfruitful until late in the season, when they produced a fair number of pubescent, nearly seedless fruits weighing from 0.5 to 3.0 grams. The skin was

colorless, and the flesh was pale orange-yellow. To reduce crowding, several plants were cut off just below the soil surface. Regeneration of shoots occurred from roots remaining in the soil, a process not observed in cultivated tomatoes.

Examination of the pollen mother cells of 13 of the 45 plants described above, showed all to be triploid. Four other plants which were exceptional in appearance also proved to be triploid. The number of trivalents at diakinesis was similar to that observed in triploid cultivated tomatoes. The pollen sterility and unfruitfulness of this family were apparently due to the presence of 12 extra chromosomes. The finding of two tetraploids among 24 F_1 plants and the strong resemblance of the triploid plants to *dentatum* suggest that the triploids may have originated from a tetraploid F_2 plant pollinated by a diploid plant of *dentatum*.

Summary

In a line originating from a single seed of a wild race of *Lycopersicon peruvianum* var. *dentatum* Dun. (*L. chilense* Dun.), two seedlings were completely sterile; the third was fertile.

In the pollen mother cells of the sterile plants, the 12 pairs of chromosomes were greatly elongated at first metaphase and usually entangled. At first anaphase many strands connected the two plates, and lagging pairs, single chromosomes, and fragments occurred commonly.

In the fertile plant, meiosis was normal in the pollen mother cells except in hot weather, when the chromosomes tended to be unpaired at diakinesis and nonreduction occurred as a result. Pollen from this plant gave F_1 hybrids with *L. esculentum* and with F_1 *esculentum* × *pimpinellifolium*. Of the F_1 plants, 84 were diploid, with normal meiosis; two were tetraploid. In the tetraploid plants, from three to nine quadrivalents were observed at first metaphase, as in the autotetraploids of *L. esculentum*.

All F_1 plants were extremely vigorous but only partially fertile. The canescence, leaf shape, presence of pseudostipules and bracts, and pubescence of the fruit of *dentatum* were partially dominant. Apparently, *dentatum* contains a gene, or genes, which partially inhibit the effects of the *Y* (yellow-skin) and *R* (red-flesh) genes of cultivated tomatoes. In the ripe fruit of the F_1 hybrids, pigments of the carotene class probably predominated and only a little lycopene was present.

A population of triploids from open pollination of an F_2 hybrid resembled *dentatum* much more closely than *esculentum* and may have originated from a tetraploid F_2 plant pollinated by a diploid plant of *dentatum*.

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THOSE DROSOPHILA SIBS

Wartime proofreading got into a last-minute note in the June Journal (Page 178), on a monograph listing and describing Drosophilidae of Texas and neighboring states. Four times Drosophilidae became *Drosophilae*. It was also said in the original script that N. Y. A. projects could and *did* advance science. There were a couple of minor "typos"; all in all something of a record.—Ed.

A NEW LOCALITY FOR TEOSINTE IN MEXICO

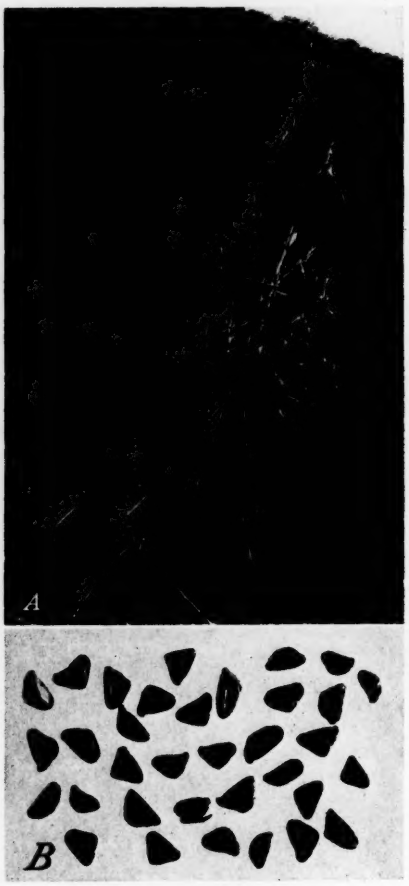
TEOSINTE (*Euchlaena mexicana* Schrad.) has been found growing as a wild plant at several locations in Mexico and Guatemala. Collins* stated that in Mexico it had been found as a wild plant only in cultivated areas but Kempton and Popenoe† found it growing wild outside such areas in Guatemala. While in Mexico in 1941, the writer found teosinte growing wild in a region not previously reported in the literature. On account of the interest in this plant as a possible progenitor of maize, this note is to put the new location on record.

En route from Acapulco to Mexico City by automobile on December 12, teosinte was first observed growing along the roadside at the bottom of a small mountain valley at km. 329.5, about 29.5 km. southwest of Chilpancingo in the State of Guerrero. Much of the seed already had shattered from the plants, but that collected was typical of Mexican teosinte. Photographs of some of the plants growing at that point and of the seed harvested are shown in Figure 7.

Continuing toward Chilpancingo, teosinte was observed growing along the rocky mountain sides for a distance of about three km., much of it far from any cultivated fields. The extent of the distribution to the southwest was not determined. Dr. L. F. Randolph, informed of the discovery on his way to Mexico, visited the same area and reports teosinte plants for a similar distance along the road toward Acapulco.

With the exception of the Chalco site in the Valley of Mexico which had no drainage to the sea, all localities for teosinte in Mexico are in the Pacific Watershed and this new location is no exception. Teosinte has never been found wild below 3,000 ft. and, although the elevation of this new site is not available, it is probably only a few hundred feet lower than Chilpancingo, viz., 4,532 ft.

It seems remarkable that teosinte was not reported long ago in this particular area, as it lies along the earliest Spanish route across Mexico, extending from Vero Cruz to Mexico City, thence to Acapulco.



WILD TEOSINTE
Figure 7
Plants and seeds of teosinte from Guerrero, Mexico.

MERLE T. JENKINS
U. S. Department of Agriculture

*COLLINS, G. N. Teosinte in Mexico. *Jour. Hered.* 12:338-350. 1921.

†KEMPTON, J. H., and WILSON POPENOE. Teosinte in Guatemala. *Carnegie Inst. of Wash. Pub. No. 483:* 199-218. 1937.

AN IDIOPATHIC CONVULSIVE DISORDER WITH DETERIORATION

Apparently Dependent upon an Incompletely Sex-Linked Gene—Studies in Human Inheritance XXIII

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Departments of Zoology and Entomology, and Medicine
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RECENTLY a young man in search of advice on a peculiar problem came to the medical genetics laboratory of the Ohio State University. He was one of a family of seven children. The three boys were all normal, but the four girls were mental defectives of a unique nature. Three other cases of this defect appeared in collateral relatives (Figure 8). The individuals concerned were all Mennonites, and the boy was engaged to a Mennonite girl. He desired information as to the chances of the defect appearing in his children.

He described the defect as follows: The children are apparently normal up to the age of one year. About that time a series of spasms appears, somewhat like epileptic fits, each lasting a few minutes, followed by sleep or unconsciousness for a half hour to an hour. The spasms come in cycles: a few days of spasms, then ten days or so without them, then a few days of spasms again. The children degenerate physically and lose flesh. They also degenerate mentally. They learn to say a few words, then lose the ability. They even learn to feed themselves, and then lose that ability. Some walk a little at first. They finally "have no mind." Death occurs between four and twelve years of age.

At the time of the young man's visit, three of his sisters were dead, and the fourth (VII, 15) was eight years old, a helpless idiot. The symptoms of the sisters and cousins were so strikingly similar that no doubt could exist of the unity of the condition in all the affected children. A visit was made to the home of the parents, and the living affected child was examined.

Case History

Past History

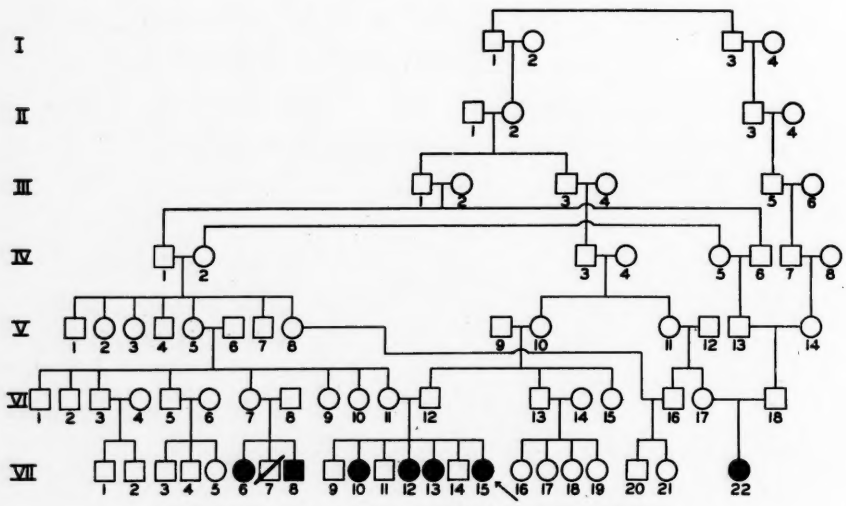
The patient is a white female child aged eight years and five months at the time of the examination (September, 1942).

She was a full term baby weighing about seven pounds and was delivered without any unusual occurrences. The maternal health during the pregnancy was not remarkable. The baby seemed to be normal at birth, and appeared to have an average development during the first few months of her life. At one year of age she walked "on all fours," and at sixteen months she walked erect. At the latter age she fed herself, played with her toys, and knew the members of her family. Her speech was limited to single words. She was right-handed.

The illness was marked by an abrupt and unexpected onset at 26 months of age in the form of a convulsive seizure similar to those which had occurred in the illness of her sisters. This initial seizure was very similar to the large number of convulsions which she has had since that time. This first convulsion appeared early in the morning and was marked by a sudden loud cry, a drawing of the face, a flexion of all four limbs and violent shaking. This attack lasted for a couple of minutes.

After the first convulsion the child deteriorated and the downhill course has been more pronounced since the age of four years. There have been no serious illnesses and no accidents. She sleeps well.

The ability to speak single words was lost during the third year. During that



PEDIGREE OF A NEW CONVULSIVE DISORDER

Figure 8

A pedigree of a new syndrome in man, idopathic convulsive disorder with deterioration. Affected individuals are indicated by the sold square and circles. The cross-lined square (VII, 7) indicates an individual who died at birth.

period, however, she was active, investigative and playful.

As the decline continued she had periods of marked and continued laughter or weeping but these gradually diminished and are no longer exhibited. Since the age of six she has made little sound except for a loud cry at the beginning of the attacks. She hears sounds, and is even over-sensitive to noises. She also appears to see objects and will at times pick up small bites of food and place them in her mouth. However, she is almost totally helpless and has to be fed with soft foods. There has been little or no difficulty with deglutition. She has been fed well but has gained almost no weight in the last two years.

Present Status

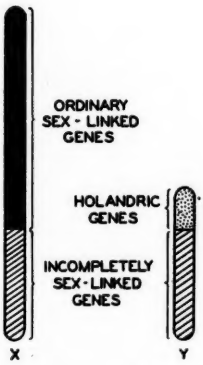
The condition of this patient at eight years and five months of age may be described under two headings, (1) interval condition and (2) condition during an attack.

(1) *Interval condition.* During the past two years the longest intervals between attacks have been 10-14 days. As a rule there are several attacks each day. The longer intervals appear to be followed by unusually severe attacks.

The expression of the face is blank, staring and unresponsive. The gait is slightly unsteady; the most marked alterations are stumbling and swaying or weaving. The head is carried in a slightly flexed position, or is jerked forward and then upward. There is some kyphosis or stooping. The upper limbs are held up like the wings of a bird and are waved or flapped when she walks. She toes inward and there is some forward propulsion but she does avoid obstacles. In a large room she circles counter-clockwise for several rounds. Then she suddenly assumes a squatting position and will maintain this for a long period. During a considerable amount of the time she sucks her fingers or bites her clothing.

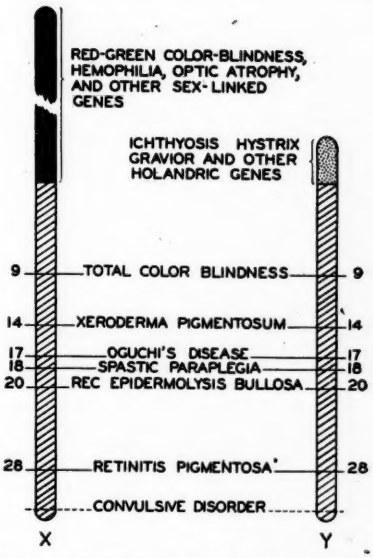
The child showed no cooperation during the examination. On the other hand she offered no particular resistance.

The weight was 34 pounds. The pulse



THREE DEGREES OF SEX-LINKAGE
Figure 9

Diagram of the sex chromosomes of man, showing the location of the three types of genes associated with these chromosomes.


RED-GREEN COLOR-BLINDNESS, HEMOPHILIA, OPTIC ATROPHY, AND OTHER SEX-LINKED GENES
ICHTHYOSIS HYSTRIX GRAVIOR AND OTHER HOLANDRIC GENES
9 TOTAL COLOR BLINDNESS 9
14 XERODERMA PIGMENTOSUM 14
17 OGUCHI'S DISEASE 17
18 SPASTIC PARAPLEGIA 18
20 REC EPIDERMOLYSIS BULLOSA 20
28 RETINITIS PIGMENTOSA 28
CONVULSIVE DISORDER
X
Y

LINKAGE MAP OF SEX-LINKED GENES
Figure 10

A map of the sex chromosomes of man, based on the work of Haldane. The gene described in this paper is added to the map without specifying its exact location.

was 90 and the respirations were 22. Eye movements were conjugate and there were no ocular palsies. The pupils were round and equal and the direct and consensual pupillary reflexes were elicited. There was a normal optic fundus reflex and there were no abnormal pigmented spots in the retinae. Both optic discs showed physiological cupping.

The motor components of the fifth (trigeminal) and seventh (facial) nerves were active bilaterally. The soft palate was motile and in midline position. The tongue was protruded in the midline. The external auditory canals were not remarkable.

In the neck there was nothing unusual. The sterno-mastoid muscles appeared to be prominent and powerful. There were no heart murmurs. The abdominal reflexes and all the deep reflexes could not be obtained. The right planter response was definitely flexor while the left one was definitely extensor.

Summary. The unusual findings were an absence of all deep reflexes and the presence of a planter extensor response of the left side.

(2) *Condition during an attack.* The attack is usually announced by a long sharp cry. She has had "hundreds" of them, the majority of which have occurred at night or when she was eating. The eyes roll about at first and later in the attack are pulled upwards until the iris is hidden beneath the upper lid. Her head is pulled to the right. The forearms are usually flexed but sometimes the entire right upper limb (except the hand) is in extension or even in hyperextension. Both fists are always clenched. The lower limbs show flexion at both the hip and knee joints. Often there is frantic kicking and violent shaking which rocks the bed. A typical convulsion lasts one minute or a little longer. However, they may be drawn out for as long as

three hours. Vomiting is unusual and biting of the tongue is rare.

There is usually some gritting of the teeth, sometimes she urinates and rarely she defecates. A second attack may follow in 20 or 30 minutes and she may average two or three an hour for two or three days. Afterwards she is quite weak for a day or two and then seems to regain her usual level.

Clinical Diagnosis

It is not possible to make a satisfactory diagnosis in the absence of the pathological specimen. Examination of the brain has been arranged for at the child's death. The condition is clinically most similar to the various forms of diffuse cerebral sclerosis sometimes erroneously lumped under the general heading of Schilder's disease. Schilder's disease is now classified with the encephalitides and considered non-hereditary, while three forms of hereditary degeneration of the cerebral white matter are recognized. They are pathologically similar, though clinically distinct. They comprise the acute infantile form described by Krabbe,[5] the subacute juvenile form presented by Scholz,[8] and the chronic form of Pelizaeus[7] and Merzbacher.[6]

The condition presented here differs clinically from all three types previously described. In the acute infantile form, the onset is about the fifth month of life, optic atrophy and impaired hearing are involved, and the course is rapid, leading to death within the first year. In the subacute juvenile form, the onset is not until about the eighth year, and starts with deafness, followed by failure of vision, pallor of the optic nerves, and dementia. Death occurs within two years of the onset of symptoms. In the chronic form the earliest symptoms (wheel nystagmus and rotary head movements) may appear as early as three months, but mental deterioration does not begin to become evident until about six years of age. The course of the disease is very slow, with progressive weakness and inability to walk. Patients may reach middle age, and males have been more commonly affected than females.

The signs and symptoms of the case presented here point towards an eventual pathological and clinical diagnosis of a new form of diffuse cerebral sclerosis or some similar heredo-degenerative disorder. Until such time as the pathological specimen is available the best possible clinical diagnosis is idiopathic convulsive disorder with deterioration.

Genetic Analysis

Inspection of Figure 8 reveals that the trait is apparently the result of a recessive gene substitution, and the peculiar sex distribution of the trait raises the possibility that the gene is incompletely sex-linked. Genes of this sort are carried on the homologous regions of the *X*- and *Y*-chromosomes, and may undergo crossing over (Figure 9).

Following the pioneer cytological work of Koller and Darlington,[4] six incompletely sex-lined genes in man have been established by the work of Haldine,[2,3] and their positions have been mapped (Figure 10). A gene of this nature will behave as an ordinary autosomal factor except for one thing: it will be differentially transmitted to the male and female offspring of a male parent heterozygous for the gene. A male of this sort will tend to transmit such a gene to offspring of the same sex as the parent from whom he received it.

In the case of a dominant gene, this form of behavior is readily recognized, and crossovers are directly detectable. When a recessive gene is involved, however, the incomplete sex-linkage is more difficult to detect, since in any particular instance it can not readily be determined whether a heterozygous father received the gene from his father or from his mother. The analysis in such cases is therefore not by direct observation, but by an adaptation of Fisher's[1] u-score linkage method for recessive traits.

In certain instances it may be possible to facilitate the analysis because of known consanguinity in the family, with consequent indication of the source of the gene in a heterozygous father. The present pedigree is of this nature, and an examination of Figure 8 will indicate

that the parents of the propositus (VI, 11 and 12) are third cousins, *related through the father's mother*. This substantiates the inference drawn from the sex distribution that the gene is incompletely sex-linked; since a man receiving the gene from his mother will tend to pass it on to his daughters, and will transmit it to his sons only as a result of crossing over.

Because the gene involved here is obviously recessive, the affected girls are all non-crossovers, but the unaffected sons are not necessarily non-crossovers, since one or more of them may have received the gene in heterozygous state as a result of crossing-over in the father. Haldane appears to have missed this point. In his paper on the incompletely sex-linked nature of spastic paraplegia,[3] apropos of a family in which the parents were related through the father's mother and in which there were two affected daughters and two unaffected sons, he he says (page 142) "There were thus no cross-overs. . . ." This statement is obviously not justified.

If the crossover percentage be represented by c, the probability that a normal son will carry the gene on his Y-chromosome as a result of a crossover from the X- to the Y-chromosome of the father is given by $\frac{c}{2-c}$.

In the present pedigree (Figure 8), a sister (VI, 7) of the mother of the propositus produced two children with the defect. A third child (VII, 7) died at birth. The husband of this woman had the same surname as the woman's mother (the family name of generations III and IV), and although he came from a neighboring state and no relationship was known, he too was a Mennonite, and a relationship very probably exists, as both are heterozygous for the gene in question. Of the two living children, one is a crossover and one a non-crossover on the assumption that the gene is incompletely sex-linked, no matter from which of his parents the father received the gene.

A first cousin (VI, 17) of the father of the propositus also had an affected daughter. This cousin married a man (VI, 18) of the same family name mentioned above (the family name of III, 1 and 3, and IV, 3, 5 and 6). He was related to his wife both through his father and through his mother, so that it can not be said whether he carried the gene on his X- or his Y-chromosome. The daughter (VII, 22) could therefore be either a crossover or a non-crossover.

It thus becomes impossible to make any estimate of the crossover frequency in this pedigree, and, indeed, it can not be insisted that the gene is located on the homologous portions of the sex chromosomes at all. The peculiar sex distribution of the trait in the family of the propositus, however, coupled with the fact that the parents are related in precisely the manner that would be necessary to produce this particular sex distribution of an incompletely sex-linked gene, make it a reasonable inference that the gene is located on the homologous portions of the X- and Y-chromosomes.

To return to the original problem, which was the advice to be given to the young man, it can be said with certainty that the gene is recessive. If it were an autosomal recessive, the chances that the man carried the gene would be two out of three. If the gene be considered as incompletely sex-linked, the chances are greater than one out of two and less than two out of three (the exact probability being $\frac{1}{2-c}$ where c represents the crossover frequency). The fiance of the young man is a Mennonite girl; while no relationship is known, the Mennonites form a comparatively small group, and a common ancestry is not unlikely for these two persons. The probability of such a common ancestry must therefore be the determining factor in making the genetic prognosis.

Summary

A new syndrome in man is described, clinically diagnosed as idiopathic convulsive disorder with deterioration. The

trait appears to be dependent upon a recessive lethal gene substitution, and the peculiar sex distribution of the trait in the pedigree presented suggests the possibility that the gene is incompletely sex-linked, located on the homologous portions of the sex chromosomes.

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BIOCHEMISTRY AND TEMPERAMENT IN THE AGOUTI RAT

To the Editor:

I have just received the November, 1942, issue of the Journal of Heredity, and was greatly interested in the paper by Clyde E. Keeler on the Association of the Black Gene with Behaviour in the Norway Rat. I would like to quote a few references, and possible conclusions that may be drawn from them.

(1) Grey rats are more savage than black. (Keeler: Journal of Heredity, Nov., 1942.)

(2) White rats have sufficient extra adrenal tissues to survive extirpation of the glands. (Hoskins: *Endocrinology,* page 26.)

(3) Bloch and his co-workers suggested that all pigmentation is due to the presence of a specific oxydase in the skin, which forms melanin from 3-4-di-hydroxyphenyl-alanine. They expressed the belief that the latter substance is one of the normal precursors of epinephrine; and that when, in consequence of the destruction of the adrenals, epinephrine fails to be formed, these substances accumulate in the skin and are converted into pigment. (Quoted in A Clinical Study of Addison's Disease; Rowntree and Snell; page 173.)

(4) According to Cannon, epinephrine is responsible for the phenomena of rage. (Cannon in Barker's *Endocrinology and Metabolism.*)

From the above statements I would suggest the following scheme (it is too much like guesswork to be given the dignity of an hypothesis) for investigation: Black rats have less chromaffin tissue than grey ones. They therefore manufacture less epinephrine. As a consequence they are less savage. Also, less of the normal precursors of epinephrine will be used in its manufacture, therefore there will be more available for pigment formation. So that the rats are black. Finally, the gene which is responsible for the association of coat colour and behaviour is not pleiotropic in its action, but controls the amount of chromaffin tissue present in the body.

I would like very much to investigate this myself, but as I am at present in the navy it is not possible. However, it may come to the notice of someone who has the necessary time (and money) and interest to do so. It would be a tremendous undertaking. I know of no definite evidence for the statement that black rats have less chromaffin tissue than grey (the suggestions of Keith and Stockard are of interest in this connection), and the estimation of the total amount of this tissue present in even one rat would be quite a lengthy process. However, I would like to make one more quotation to indicate the importance of the subject, from Haldane's *New Paths in Genetics,* 1941: "in fact, the colours of animals and plants are indices of their metabolic processes, and though colours may have a protective value, this is not necessarily the basis of their selective value."

Yours faithfully,

A. J. Lea.
(*Surgeon Lieutenant, R.N.V.R.*)
"Four Winds"
Stourport-on-Severn
England

Comment by Dr. Keeler

I have always believed that there are a number of intermediary paths between the black locus or any gene locus and the correlated effects on behavior. Surgeon Lieutenant Lea has pointed out what may be one of the important paths because of the known effects of the adrenal upon both pigment development and behavior.

The work of Shopbach, Keeler and Greenberg (*Growth* 7:83-95, 1943) was directed toward looking for a tie between thyroid size, behavior, and basal metabolism. We assumed that a

(*Continued on page* 217)

A LETHAL EMBRYONIC WING MUTATION IN THE DOMESTIC FOWL

NELSON F. WATERS AND JAMES H. BYWATERS*

EACH year embryonic mortality, in the poultryman's lexicon, "eggs that fail to hatch," costs the poultry industry several millions of dollars. Such mortality is due to a combination of causes, chief among which are management, nutrition, and genetics. It would be difficult to appraise the mortality due to inherent defects alone, but the loss must be considerable. There are several genetic lethals for which the mode of inheritance is known. Increased examination of embryos failing to hatch will undoubtedly uncover many more.

All unhatched eggs are examined routinely in the viability studies conducted at the U. S. Regional Poultry Research Laboratory. Of the original ten strains of Single Comb White Leghorns introduced into the Laboratory, all have shown the presence of one or more genetic lethals. The fact that these strains were obtained from widely separated regions of the country would suggest the widespread occurrence of lethal genes. It is the purpose of this paper to report the occurrence of a new embryonic lethal mutant termed "wingless."

Description of Wingless

The wingless chicks were either completely devoid of both wings or had vestigial wing appendages on one or both sides (see Figure 11). In addition to the wingless condition, the lungs, air sacs, and kidneys were partially or completely absent (see Figure 12). The rear appendages showed numerous deviations from normal. The down plumage of all wingless embryos was abnormal. The abnormal embryos were apparently equal in size to their normal sibs. The defect may be observed as early as the fourth day of incubation. Many of the embryos are still alive at the end of the 21st day of incubation. A more complete description of the morphological differences follows:

Wing Appendages: The majority of defective embryos shows no wing development. Vestigial wing appendages on one or both sides, ranging from only rudimentary humeri to nearly complete wings, appear occasionally on a few embryos. In some instances the rudimentary humeri are present but fail to evaginate through the outer body surface. Absence of wing buds may be determined by the fourth day of incubation.

Posterior Appendages: Numerous morphological deviations from normal rear appendages occur in connection with the wingless condition. All wingless embryos are syndactylous whenever the third and fourth digits are present. Frequently, toes are missing or duplicated, the halex, or first toe is misplaced, the scales on shanks and toes are quite rudimentary, down feathers are present on shanks and toes, and ankylosis of the hock joint is present.

In addition to the above named abnormal conditions appearing in the rear appendages, many minor ones exist.

Respiratory System: Only a small part of the lung tissue is present. In most instances the pulmonary cavity is empty or occupied by adjacent viscera. In a few embryos the pulmonary cavities contain a serous fluid confined by the serous membrane. The primary bronchi are present and in all cases examined ended in a sealed, blind pouch. Air sacs have not been found in any of the embryos examined.

Urogenital System: Examination of a large number of defective embryos shows in most cases no development of the metanephros, or definitive kidney. In a few instances, however, a scattered

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NORMAL AND "WINGLESS CHICKS"

Figure 11

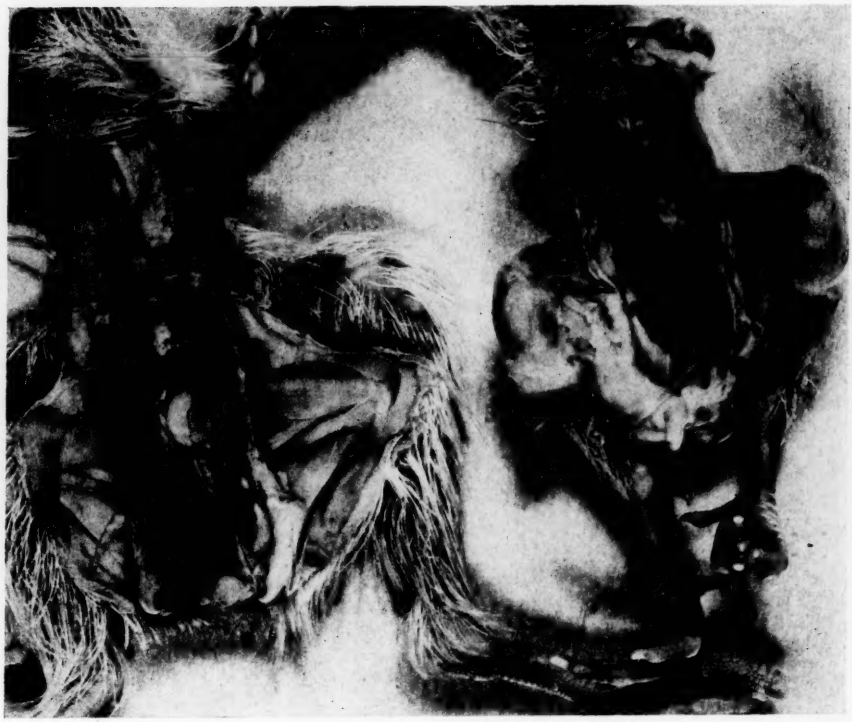
Comparison of normal, "vestigial wingless," and complete "wingless" chick embryos. The two grades of wingless embryos reach the hatching stage but fail to emerge. In addition to the external defects of wings, feet, and feathers, the internal structure of these chicks is also very abnormal (See Figure 12).

series of metanephrogenous tissues may appear. The development of this metanephrogenous tissue at 21 days is approximately equivalent to the development found in a normal 5 to 7 day old embryo. The mesonephros is well defined in the wingless embryo at 21 days although degeneration of this tissue may be comparable to that found in the normal 21 day embryo. Male and female gonads appear to develop normally.

Plumage: All wingless embryos show the abnormal feather condition described by Lepkovsky et al[2] as "clubbed down." The down condition has a small bulbous mass which is filled with a gelatinous-like substance, near the base of the shaft. In addition the down feather, in many cases, fails to rupture the surrounding sheath. This down condition is not uncommon and is frequently associated with apparently normal embryos.

Experimental

The wingless abnormality is inherited as a simple autosomal recessive. Figure 13 shows the pedigrees of all birds involved in the study of wingless. The two parental birds, *A357*E_2 and *A1221*, were from two different strains. During the year 1940, male *A357*E_2 was bred to female *A1221* producing 94 progeny which represented 91.3 per cent hatchability of fertile eggs set. Examination of the unhatched embryos from this mating showed no dis-



INTERNAL DEFICIENCIES OF WINGLESS EMBRYOS

Figure 12

On the left is a dissected normal embryo for comparison with the wingless on the right. Note the absence of lung tissue of wingless and the partial development of the excretory system. A surprising variety of organs is involved in this syndrome conditioned by a single gene.

cernible abnormalities. The following year (1941) a son, *B10H*, resulting from this mating, was mated to eleven sisters. Five of the sisters produced the wingless condition, while the other six sisters gave only normal embryos. It is important to note that if inbreeding had not taken place at this time, this recessive character, due to the closed system of mating in practice at the Laboratory, would have soon become widespread in the flock before it could have been dicovered.

A total of 111 normal chicks, or embryos, and 30 wingless embryos were observed. A "chi square" analysis (Table 1) of the matings producing the wingless condition on the basis of a 3:1 ratio substantiates the hypothesis of a simple autosomal recessive.

Inasmuch as both the progeny and relatives of $A357E_2$ and *A122I* were used extensively in the 1941 matings, we were greatly concerned as to the diffusion of this recessive lethal in the flock. The original mating and resulting progeny did not disclose which parent was the offending heterozygote. Three of the heterozygous pullets, *B10D*, *B10C*, and $B10F_2$ were bred to another brother, *B10E*. Only normal embryos resulted from these matings. The other two heterozygous pullets, $B10H_2$ and $B10J_4$, were backcrossed to their sire, $A357E_2$, and only normal embryos resulted from these matings. The

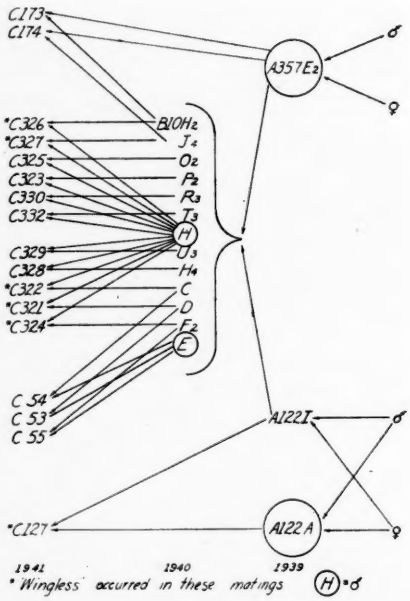
original female, *A1221*, was bred to a brother, *A122A*. This mating produced wingless embryos which would indicate that these parental sibs were heterozygous for the wingless condition, which absolved male *A357E*[2].

Discussion

It is interesting to observe that a single gene affects so many different parts and particularly so when the mode of origin of these parts is considered. All three germ layers are involved through the action of a single gene. It would not be surprising if a single gene could cause lethality early in the life of an embryo, or if numerous related parts were affected. In the present case, however, and except for those parts described, seemingly normal development takes place in those organs which have a common origin.

It would appear that more or less of a deficiency exists for certain growth substances which are necessary for regulatory and complete development of affected parts. Also, such developmental growth substances would operate early and would appear to be specific for certain organs. The wings, for example, are absent in many embryos, but are nearly complete in others. In those cases where wing development is well advanced there are corresponding developmental advancements in the other affected parts. All abnormal embryos die at hatching time or soon thereafter. Thus, while wingless is inherited as a simple recessive lethal, the degree of development of parts varies considerably.

The fact that seemingly unrelated organs such as appendages, respiratory system, urogenital system, and plumage are affected by the action of one pair of alleles would suggest a common hormonic control of growth and differentiation. Of equally speculative importance is the possibility that other combinations of parts and organs may be associated with other hormones. Goldschmidt[1] presents a résumé of similar cases of the multiplicity of gene action on growth and differentiation of individual parts.



PEDIGREE OF WINGLESS CHICKS

Figure 13

This chart shows the relationship of all the wingless birds which were observed. By analysis of this pedigree it was possible to determine which of the ancestors were "carriers." Elimination of their progeny avoided the wide dissemination of this defect in the flock.

Summary

Routine examination of all unhatched eggs from a flock of Single Comb White Leghorns at the United States Regional Poultry Research Laboratory discloses the presence of an embryonic lethal which has been termed "wingless." This abnormality is inherited as a simple

Table I. Chi-Square Analysis of Wingless Matings on the Basis of a 3:1 Ratio

Hen	Fertile Eggs set	Normal embryos		Wingless embryos		χ^2
		Observed*	Expected	Observed	Expected	
B10C	25	22	18.75	3	6.25	2.36
B10D	24	18	18.00	6	6.00	0.00
$B10T_2$	31	24	23.25	5	7.75	1.30
$B10R_3$	24	18	18.00	6	6.00	0.00
$B10J_4$	37	27	27.75	10	9.25	0.08

* Includes the chicks that hatched.

autosomal recessive. In addition to the wingless condition, the lungs, air sacs, and definitive kidney may be partially or completely absent. The rear appendages show numerous deviations from normal and the down plumage in all cases is abnormal.

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TEMPERAMENT IN THE AGOUTI RAT

(*Continued from page 212*)

high basal metabolic level would be found in grays because of their larger thyroids, plus greater savageness and activity. We were surprised to find actually the opposite; namely that mutants have much higher metabolic rates than do grays. The conclusion is that grays burn their fuel most efficiently as a result of natural selection in the wild (and that color mutations reduce this efficiency). So it may well be that Lea's suggestion will uncover the outstanding path, since complications have arisen with the thyroid clue that looked promising.

The approach chosen by Shopbach, Keeler and Greenberg was suggested by the data given in a chart on page 245 of the paper by Keeler and King (*Jour. Comp. Psychol.* 34:241-250). This chart shows that mutant albinos, piebalds and blacks have smaller thyroids than do grays,—black thyroids being astonishingly small. Correspondingly, blacks were estimated as almost nil in savageness and wildness. That all mutations are low on voluntary exercise is shown by the chart. It also shows that thyroids, hypophyses, suprarenals and gonads of albinos are slightly smaller than "wild type." For browns all of the glands are as large as for grays, save that the gonads are reduced. For blacks most of the glands are probably reduced. For piebalds, the glands are in general reduced. For curly, a very savage group, these glands are all large.

Consequently, I felt that some of the paths must lead between the coat color gene and behavior through thyroid, suprarenal and gonads. The change in voices of mutants recorded and analysed with the collaboration of Showers and noted by Keeler and King (*ibid*) also suggested a functional alteration, possibly of the thyroid.

But there must also be paths between coat color genes and behavior that lead through the nervous system, since there is a general reduction in brain size in mutants. The chart referred to above shows paraflocculi and olfactory bulbs reduced in mutants, and my general observation is that mutants are never so disturbed by the presence of strangers as are grays. It was noted in the paper by Keeler (referred to by Lea) that albinos may be greatly deficient in the sense of smell.

I believe it highly important to support not only the research that Surgeon Lieutenant Lea has suggested, but also the complete program of exploring all the paths, anatomical and physiological, that lead between the coat color genes and behavior.

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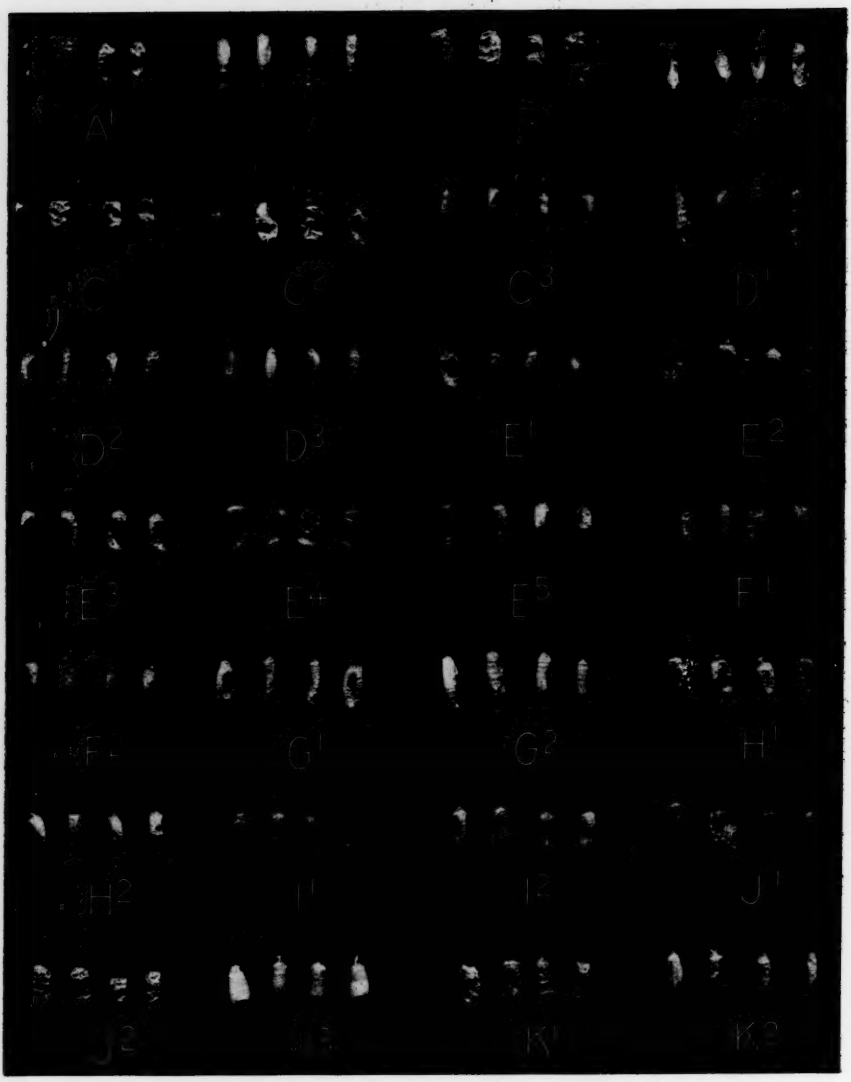
Familial Syringomyelia

Recently we had an opportunity to study four brothers in a family each disabled by a disorder of the lower extremities characterized by (1) exaggerated callus under the great toe, insidious in appearance; (2) progressive ulceration at the site of the callus, eventuating in amputation at various levels, and (3) anesthesia of varying extent in the part involved.

The condition reported herewith is variously known as familial neurotrophic osseous atrophy, status dysraphicus, myelodysplasia and syringomyelia. No definite causative agent has been disclosed. In the cases under discussion the familial background is striking. Four male siblings and three male relatives have similar, if not the same, disease. * * *

The clinical picture of intractable callus forming under the large toe, tending to erode and ulcerate and to be associated with progressive anesthesia of the affected extremity, is uncommon. When known to affect other male members of the family tree the diagnosis of syringomyelia or one of its synonyms is always more than likely. The only diseases to be differentiated are syphilis, tuberculosis, osteomyelitis and leprosy. The first three are ruled out on clinical and laboratory evidence. One of us (C. R. M.), who has had clinical experience with leprosy, felt that these cases did not fall into this category.—COLONEL CHARLES R. MUELLER and MAJOR SAMUEL J. SUGAR. *Jour. A. M. A.*, July 10, 1943.



SEEDS OF WHEAT × AGROPYRON HYBRIDS

Figure 14

The seeds shown from *A* to *I* are hybrids of *T. durum* and *Agropyron;* and the remaining seeds are hybrids with *T. aestivum*. A^1—Acme × *Agropyron intermedium;* A^2—Acme; B^1—Arnautka × *A. trichophorum;* B^2—Arnautka; C^1—Barnatka × *A. trichophorum;* C^2—Barnatka × *A. trichophorum;* C^3—Barnatka; D^1—Marouani × *A. intermedium* (type A); D^2—Marouani × *A. intermedium;* D^3—Marouani; E^1—Mondak × *A. intermedium* (type A); E^2—Mondak × *A. intermedium;* E^3—Mondak × *A. intermedium;* E^4—Mondak × *A. trichophorum;* E^5—Mondak; F^1—Nodak × *A. intermedium;* F^2—Nodak; G^1—Peliss × *A. intermedium;* G^2—Peliss; H^1—Pentad × *A. trichophorum;* H^2—Pentad; I^1—Mosida × *A. intermedium* (type A); I^2—Mosida × *A. intermedium;* J^1—Rex × *A. intermedium;* J^2—Rex × *A. trichophorum;* J^3—Rex; K^1—Turkey-Florence × *A. intermedium* (type A); K^2—Turkey-Florence.

INTERGENERIC HYBRIDIZATION OF TRITICUM AND OTHER GRASSES, PRINCIPALLY AGROPYRON*

D. C. SMITH†

DURING the past ten years numerous reports have been published concerning successful hybridization of the wheats (*Triticum*) with other grasses. The primary objects of such investigations have been two: the development of perennial wheats and the isolation of large-seeded, perennial forage plants of good quality. Reports of Russian workers have indicated phenomenal results in this program. More recent studies in Canada and in the United States have verified, in part, the previous reports of compatibility of *Triticum* and certain *Agropyron* species. Though no commercially valuable segregates have become available, results have encouraged additional work.

The present paper is a summary of further investigations in crossing *Triticum* and other grass genera with particular emphasis upon hybridization of *Triticum durum* Desf. and *T. aestivum* L. with *Agropyron* species.

Review of Literature

Since 1930 extensive investigations have been concerned with hybridization of *Triticum* and other grass genera, particularly *Agropyron*. White[32] has presented an extensive list of earlier workers and Smith[21] reviewed certain literature pertinent to crosses of *T. aestivum* with other species. The present discussion will be confined to reports concerning *T. durum* except for the purpose of comparison.

Peto[18] reported $2n$ chromosome numbers of *Agropyron* species as *A. cristatum* 14 and 28; *A. dasystachyum* 28; *A. elongatum* 70; *A. glaucum* 42 and *A. tenerum* 28. *A. pungens* had an n number of 21.

Favorsky[9] stated that *A. glaucum* and *A. intermedium* are synonyms and this is also indicated by Hitchcock.[10] Khiznjak[12] reported gametic chromosome numbers of 14 and 21 in different strains of *A. intermedium*. *A. trichophorum* has a $2n$ number of 42 according to Araratian.[1] This species is also considered to be very closely related to *A. intermedium* by some workers.[31] Stebbins and Love[22] found $2n$ numbers to be 28 and 42 for strains of *Elymus triticoides*. Chromosome numbers for *Hordeum brevisubulatum* have not been reported, to the writer's knowledge.

Vakar[25] obtained hybrids in crosses of *T. durum* with *A. elongatum* but not with *A. glaucum*, *A. intermedium*, *A. repens*, and *A. tenerum*. Armstrong[2] attempted to cross *T. durum* with *A. caninum*, *A. cristatum*, *A. dasystachyum*, *A. desertorum*, *A. elongatum*, *A. glaucum*, *A. imbricatum*, *A. obtusiusculum*, *A. repens* and *A. richardsoni*. *A. glaucum* and *A. elongatum* were the only successful male parents. White[32] found only *A. elongatum* and *A. glaucum* to be compatible in crosses of *T. durum* with *A. cristatum*, *A. elongatum*, *A. inerme*, *A. glaucum*, *A. junceum*, *A. pauciflorum*, *A. repens*, *A. smithii*, and *A. subsecundum*.

Hybrids between *T. durum* and *Agroypron* species have been obtained by a number of other workers. Veruschkine and Schechurdine,[31] Veruschkine[27.28.29.30] and Kniznjak[13.14] reported hybrids of *T. durum and A. intermedium*. Tzitzin,[23] Veruschkine,[27.28.29.30] Nemlienko,[17] and Tzitzin[24] secured hybrids of *T. durum* and *A. trichophorum*. *T. durum* and *A. elongatum* were crossed by Tzitzin,[23] Veruschkine and Schechurdine,[31] Veruschkine,[27.28.29.30] Vakar,[25.26] Derzavin,[8] Armstrong,[2] Johnson[11] and Tzitzin,[24] Hybrids between *T. durum* and *A. glaucum* have been described by Tzitzin,[23] Sinkov,[20] Armstrong,[2] Johnson.[11] Nemlienko,[17] Tzitzin,[24] and White.[32] Vakar[25] failed to make this cross successfully. Tzitzin,[23] Veruschkine[28.30] and Tzitzin[24] successfully crossed *T. durum* and

*Results of cooperative investigations of the Division of Forage Crops and Diseases, Bureau of Plant Industry; Division of Nurseries, Soil Conservation Service; and Washington Agricultural Experiment Station at Pullman, Wash.

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A junceum. Tzitzin[24] reported a hybrid between *T. durum* and a strain of *A. repens*.

Armstrong[2] obtained a greater seed set in crosses of *T. durum* × *A. glaucum* than in *T. vulgare* × *A. glaucum*. White[32] reported crossing success when using *T. durum* to be about twice that with *T. vulgare* (Host.). All varieties of *T. durum* and *T. vulgare* set seed when pollinated with *A. elongatum*. Crossed with *A. glaucum* however, two of nine varieties of *T. vulgare* failed to set seed. Schneidermann[19] referred to the work of Michurin in which average percentage of seed set in crosses between *T. vulgare* and *A. intermedium* was 29.4 while that using *T. durum* as a parent was 53.6 per cent.

Tzitzin[23] and Veruschkine[27] emphasized the importance of differences in male parent strains as to successful use in hybridization. Johnson[11] and White[32] found female parents to differ greatly in ability to develop hybrid seeds. Kikot and Volkova[16] and Khiznyak[15] noted both parents to be important in success. The former also obtained varying results using different male plants within the same strain.

Veruschkine[28] and Tzitzin[23] reported percentages of seed set up to 90 and 60 respectively in some *Triticum* × *Agropyron* crosses. Kikot and Volkova,[16] in crossing *T. durum* × *A. elongatum*, obtained seed sets up to 76.3 per cent. In pollination of *T. vulgare* × *A. elongatum*, seed set ranged from .8 to 73.0 per cent. Variations were least in combinations easiest to effect. Johnson[11] in crosses of 11 varieties of *T. vulgare* × *A. glaucum*, found seed setting to vary from .4 to 34.1 per cent. In *T. vulgare* × *A. elongatum* crosses two of three female parents set no seed while the third ranged from .2 to 4.5 per cent. In *T. durum* × *A. glaucum* combinations, seed set reached 5.9 per cent and in *T. durum* × *A. elongatum*, 8.1 per cent.

Observations have been made upon plumpness and germinability of hybrid seeds. Armstrong[2] observed those from *T. durum* × *A. glaucum* to be slightly more plump than those of *T. durum* × *A. elongatum*. When *T. vulgare* was the female, seeds from the use of *A. elongatum* as the male were better developed. Johnson[11] reported some "germless" seeds to be produced, possibly as a result of failure of embryo nucleus fertilization. Stimulated ovary development without fertilization was also thought to occur. White[32] cited work to indicate that the former explanation might be unjustifiable. Armstrong[2] and Johnson[11] observed germination of hybrid seeds to be generally good though seedling survival differed in different crosses of *T. durum* × *A. glaucum* according to Johnson.

Methods and Materials

The cereal varieties utilized in these studies were in the species *Triticum durum* Desf. and *T. aestivum* L., and are listed with accession or cereal investigation numbers in Table II. Most of the varieties have been described by Clark and Bayles.[6] Mondak was discussed by Clark, et. al.[7] Rex was described by Clark.[5] Turkey-Florence is a hard, white-grained, late winter selection from the indicated cross.

The grass species utilized as male parents in attempted crosses of *Agropyron* species with *T. durum* were *A. cristatum* (L.) Gaertn., *A. dasystachyum* (Hook.) Scribn., *A. intermedium* (Host.) Beauv., *A. pungens* (Pers.) Roem. and Schult., *A. trachycaulum* (Link) Malte,* A. *trichophorum* (Link) Richt., *Elymus triticoides* Buckl. and *Hordeum brevisubulatum* (Trin.) Link. Most of these species have been described by Hitchcock.[10] The *A. cristatum* parents were plants of the "common type." The *A. dasystachyum*, *A. trachycaulum* and *E. triticoides* strains were collections from native stands in the Pacific Northwest. *A. intermedium*, *A. pungens* and *A. trichophorum* parent strains were foreign plant introductions. Two strains of *A. intermedium* were used. Two of these had been received with the names *A. pungens* and *A. amurense*. The latter was considerably more coarse than the usual *A. intermedium*. It possessed leaves of greater width and more glaucous, and had a more decumbent growth habit. This has been designated "type A" to compare the results with those obtained from using the more typical form. *H. brevisubulatum* (P.I. 131, 539) is also a recent introduction. This species resembles *H. nodosum* L. to some extent but is more robust, tends to be prominently glaucous, has larger florets often reddish-tinged and, though tending to shatter, has a more persistent rachis.

With the exception of *A. intermedium* and *A. trichophorum* the use of a particular (male) parent species was some-

*A. *trachycaulum* (Link) Malte is the valid name for *A. panciflorum* (Schwein.) Hitchc. of Hitchcock Manual.

what arbitrary. However, previous work had shown the existence of compatibility in crosses using the two species named. With both cereal species, a fairly large number of hybrid seeds was obtained for each of these grass parents used as a male. The technique of crossing was that usually employed for self-pollinated grains such as wheat, the *Triticum* parent being the female in all instances. Verification of hybridity was obtained by allowing the seeds to germinate and examining the resulting plants.

Results

In Table I are given the results of hybridization for all combinations attempted. A glance at the data shows successful crosses to be *T. aestivum* and *T. durum* with *A. intermedium* and *A. trichophorum*. Table II contains a more detailed summary of the successful crosses including itemization of cereal varieties and grass species. "Hybrid seeds" were considered to be only those showing incomplete development, thought to be "typical" of such crosses.

When actual crosses were obtained the seeds were generally badly shrunken though some variation existed in this respect. If seeds of the same cross varied markedly in size they were grouped into lots based upon different degrees of development and studied in these groups. In Figure 14, photographs of female parental and hybrid seeds are shown. These are representative of the respective lots. When *T. durum* was the female parent, caryopses tended to be more flattened laterally than in crosses where *T. aestivum* was used. In some hybrids this was so extreme that the grains would not rest on the back or cheeks but only on the side. Typical of this condition are Figures 14B^1, C^1, C^2 and E^4. In Figure 14A^1, C^2, I^1 and J^2, smaller seeds were obtained. Attention is also directed to the relatively long and more nearly normal grains in Figures 14D^1, D^2 and G^1. Generally the seeds of crosses with *T. aestivum*, while badly shrunken, were more nearly normal-shaped than those from use of *T. durum* as may be seen in Figure 14I^1, J^2 and K^1. Figure 14J^1 however, shows much flattened and poorly developed seeds. Among the seeds shown, those of Marouani × *A. amurense* (D^1), Peliss × *A. intermedium* (G^1), and Pentad × *A. trichophorum* (H^1) are best developed.

The point of particular interest is the variation among cereal varieties as to seed set, germination, and survival of hybrid seedlings following pollination with each of the three *Agropyron* species (Table II). While numbers of florets and seeds are relatively small and percentages variable in reliability, certain apparently significant differences exist.

T. durum crosses

In crosses with *A. intermedium* type *A*, the *durum* varieties Marouani, Mondak and Pentad set 24.2, 17.5 and 3.7 per cent of seed respectively. Golden Ball failed to set seed but few florets were pollinated. Differences in plants surviving and total plants from seed were considerable for the several varieties though again numbers concerned were small. In crosses with Marouani the seed set reached 50 per cent for some heads while for Mondak it was 40.0 per cent, and the Pentad only 3.7 per cent.

Considering crosses with *A. intermedium*, seed set percentages were Acme 7.7, Mondak 14.8, Marouani 15.0, Peliss 23.0, and Nodak 37.5. Success with Pentad was very poor. Percentages of seeds germinating and seedlings surviving in the different crosses were somewhat similar. Peliss averaged lower in survival and number of plants from seed and Mondak poorer in survival. In Mondak the percentage of hybrid seed set was as high as 80 for some heads while for Nodak it reached 60.

Percentage seed sets in crossing varities of *T. durum* × *A. trichophorum* were for Barnatka 62.1, Arnautka 59.7 Pentad 38.6, Mondak 31.8 and Marouani 1.9. The latter variety was distinctly inferior in seed setting; Barnatka and Arnautka were much better in this respect than Mondak and Pentad. In some heads, seed set in Barnatka and Arnautka reached 95 per cent. In Mon-

dak and Pentad a high of 80 per cent was obtained. In per cent of seeds germinating Mondak was low with 36.7, Arnautka next with 76.3. Other varieties exceeded 90 per cent. Seedling survival varied from 57.6 per cent in Barnatka to 100 in Marouani. Mondak, Arnautka and Barnatka were low in percentage of plants derived from seeds.

T. aestivum crosses

Somewhat comparable results were obtained with varieties of *T. aestivum* as with *T. durum*. Using *A. intermedium* (type *A*) as the male parent the percentage of seed set was high for Mosida but low for other varieties. In Mosida crosses it reached 95 per cent in some heads and for Turkey-Florence it attained 41 per cent. However, germination, survival and plants-from-seed percentages were low for Mosida as well as for Federation and Turkey-Florence crosses. With *A. intermedium* Mosida was again the most successful parent in seed setting, Rex being next in order. The former had seed sets up to 50 per cent and the latter variety up to 70 per cent for some heads. Germination of hybrid seeds for these varieties was very low. Mosida proved to be a better parent than Rex in crosses with *A. trichophorum*, with some heads of the former setting up to 87 per cent while Rex reached 27 per cent. Germination was also markedly better.

Since certain *Triticum* varieties were used with two or three of the *Agropyron* species, the crossability of the latter may be considered. Regrouping selected data from Table II a summary is presented in Table III. In percentages of seed set, prominent differences are shown in combinations of *T. durum* varieties with the *Agropyrons*. Such differences are not prominent in percentage germination and other characters. The general inferiority of Pentad with *A. intermedium* is marked, though this is based upon small numbers. In crosses involving *T. aestivum* differences are also notable, *A. intermedium* being inferior to other *Agropyrons* in most of the possible comparisons. It is not easy to establish similarities and differences in the behavior of the three Agropyron species involved in these crosses. In general *A. intermedium* (type A) and *A. intermedium* were more similar in results with Mondak; while with Pentad results with *A. intermedium* (type *A*) and *A. trichophorum* were more comparable. The latter was also the case when considering Mosida.

Averages of all of the crosses with *T. durum*, when compared with those made with *T. aestivum*, show a 20 per cent higher seed set, a 50 per cent higher germination and a 40 per cent greater number of plants from seed of which the former species was a parent. Percentages of plants surviving for the two species were about equal. The significance of the differences observed may be questioned since the varietal variations are so great.

Discussion

The data presented have confirmed the results by previous workers as to the crossability of certain *Triticum* and *Agropyron* species. They have also indicated the relative incompatibility of some combinations.

Percentages of seeds obtained for most crosses were much higher than have been reported by other investigators. White[32] obtained a maximum seed set of 55 per cent in crosses of *T. durum* with *A. glaucum*. In the present results maximum seed sets of 50, 80, and 80 per cent were observed for crosses of *T. durum* with *A. intermedium* (type A), *A. intermedium* and *A. trichophorum* respectively. In *T. aestivum* × *A. glaucum* crosses White[32] reported a maximum of 66.7 per cent of seed set. Again referring to the present results, seed sets of 95, 70 and 87 per cent were obtained in crosses of *T. aestivum* with *A. intermedium* (type *A*), *A. intermedium* and *A. trichophorum* respectively. It is unlikely that greater compatibility would be obtained in crosses of some varieties of *T. durum* or *T. aestivum* within the two species. Recently certain Russian workers have suggested the inclusion of the "higher" (crossable) forms of *Agro-*

pyron in the genus *Triticum*, to which, as was recognized by early taxonomists, *Agropyron* is closely related.

In general, seeds from hybrids with *Triticum aestivum* as the female parent were better developed than those with *T. durum*. This is in agreement with the work of Armstrong.[2] Germination of hybrid seeds, though they were badly shrunken, was remarkably good. Armstrong[2] and Johnson[11] also found this to be true. Variation among crosses as to seedling survival following germination, noted by the latter, also existed in these studies. Differences in the results obtained with several varieties used as female parents in crosses otherwise identical indicate that not only seed set but germination and subsequent survival of hybrid plants are factors in practical determination of compatibility.

It is interesting to speculate on the reasons for differential behavior of parental varieties in affecting the quality of hybrids. Assuming the varieties to be cytologically and genetically stable, as well as closely related, it might be supposed that opportunity for varietal differences to be manifested would be greatly reduced. Brink and Cooper[4] have presented a review of literature and new data as well as a comprehensive discussion of the development of the embryo and endosperm following fertilization. A marked difference was found in percentage of fertile ovules collapsing in early growth when comparing results of cross- and self-pollination of alfalfa. Boyes and Thompson[3] have shown that seed development following hybridization in the Gramineae is often prevented due to rapid, early development of the endosperm at the expense of the embryo. Differences in reciprocal crosses occurred in the relative development of embryo and endosperm and subsequent completion of caryopsis maturation. In crosses of *T. aestivum* × *Secale cereale* L., the use of Chinese wheat as the female parent resulted in somewhat irregular, but in some instances normal, development of the seeds while some failed to be differentiated. When Marquis was utilized as the female parent, no seeds were obtained. Examinations showed pollen tubes to be present in the ovary but there was no evidence of fertilization. Rye pollen germinated about 60 per cent on Chinese wheat stigmas and only 10 per cent on those of Marquis. In the latter instance germination was weaker and pollen tubes shorter. No conclusions were reached as to the specific causes of the differences observed.

That a primary cause of apparent failure of seed development following fertilization may be physiologic unbalance has been established previously by other workers. Based upon present investigations, a corollary to this appears to be that varieties closely related taxonomically may possess genetic differences in ability to combine in crosses with other species and produce viable seeds and vigorous hybrids.

Summary

Results of attempts to hybridize *Triticum aestivum* and *T. durum* with *Agropyron, Elymus,* and *Hordeum* species have been reported. Crosses obtained include only *T. aestivum* and *T. durum* combinations with *A. intermedium* strains and *A. trichophorum.*

Data that have been presented indicate differences in seed formation, germination and seedling mortality to exist depending upon the male and female combinations considered. Possible reasons for such differences were not determined.

Durum varieties were more generally compatible in crosses than were common wheat varieties, though much depended upon varieties, as Mosida (*Triticum aestivum*) was about equal to the *durum* varieties used most successfully.

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*Several of the Russian authors are cited with various spellings. The variants are given in parenthesis in the citations.

Table I. Results of attempted hybridization of *Triticum durum* and *T. aestivum* with other grasses

Grass species	No. of wheat varieties	Florets pollinated	Hybrid seeds
Triticum durum			
Agropyron smithii	4	524	100
" *cristatum*	3	663	0
" *dasystachyum*	4	434	0
" *intermedium*	4	976	1167
" *trachycaulum*	2	604	0
" *trichophorum*	5	937	586
Elymus triticoides	3	250	0
Hordeum brevisubulatum	3	586	0
Triticum aestivum			
Agropyron smithii	2	973	97
" *dasystachyum*	2	180	0
" *intermedium*	5	1188	91
" *junceum agropyron*	1	98	0
" *trichophorum*	4	818	150

Table II. Comparison of seed setting with varieties of *Triticum durum*, and *T. aestivum* when pollinated with each of three Agropyron species.

Wheat species and variety	Acc. No.[1]	Total florets pollinated	Hybrid Seeds No.	Hybrid Seeds Percent	Germinated No.	Germinated Percent	Plants survived No.	Plants survived Percent	Plants from seed Percent
Triticum durum			*Agropyron smithii*						
Golden Ball	220	34	0	—	—	—	—	—	—
Marouani	218	322	78	24.2	78	100.0	44	56.4	56.4
Medak	7297[2]	114	20	17.6	19	95.0	15	82.4	82.0
Pentad	209	84	2	2.7	2	100.0	2	100.0	100.0
			Agropyron intermedium						
Acme	211	234	16	7.7	16	100.0	16	88.9	88.9
Marouani	218	80	12	16.0	12	100.0	11	91.7	91.7
Medak	7297	216	37	16.8	31	98.9	20	64.5	62.5
Medak	242	222	67	27.5	64	95.6	51	80.7	80.4
Pelico	210	74	17	23.0	14	82.4	11	78.6	84.7
Pentad	209	40	1	2.5	0	—	—	—	—
			Agropyron trichophorum						
Armautka	213	260	215	82.7	202	78.3	96	58.6	44.7
Barnatka	6214[3]	68	36	52.1	33	91.7	19	57.6	52.8
Marouani	218	186	3	1.9	3	100.0	3	100.0	100.0
Medak	7297	194	43	21.2	18	88.7	15	88.3	30.6
Pentad	209	210	8	28.0	20	98.8	86	88.8	87.9
Triticum aestivum			*Agropyron smithii*						
Federation	77	226	5	2.1	4	80.0	2	87.0	40.0
Medak	242	88	34	38.6	17	50.0	12	70.6	35.3
Red Russian	43	127	2	1.6	2	100.0	2	100.0	100.0
Ridit	248	104	2	1.9	2	100.0	2	100.0	100.0
Turkey-Florence 10080[4]	674	84	11.6	39	72.2	27	69.2	80.0	
			Agropyron intermedium						
Marquis	57	294	10	7.5	9	90.0	6	67.0	60.0
Medak	242	130	35	26.4	7	21.2	5	71.4	15.2
Red Russian	43	228	9	6.0	9	88.9	7	87.5	77.8
Rex	276	243	20	10.0	5	12.5	2	60.0	8.1
Ridit	248	134	0	—	—	—	—	—	—
			Agropyron trichophorum						
Medak	242	194	111	57.2	91	87.0	72	79.1	64.9
Rex	276	248	19	7.7	6	31.1	6	100.0	31.1

[1] Accession number, Division of Cereal Crops and Diseases, Bureau of Plant Industry, U.S.D.A. Cereal Investigations No. * [2] [3] [4]

Table III. Percentage of seeds set, their germination and survival of hybrid plants after pollination of varieties of *Triticum durum* and *T. aestivum* with Agropyron species.

Character and male species	*T. durum* Marouani	*T. durum* Medak[2]	*T. durum* Pentad	*T. aestivum* Medak	*T. aestivum* Rex	*T. aestivum* Ridit
Percentage seed set						
A. smithii	24.2	17.6	2.7	38.6	-	1.9
A. intermedium	16.0	16.8	2.5	26.4	10.0	0.0
A. trichophorum	1.9	21.2	28.0	57.2	7.7	-
Percentage germination						
A. smithii	100.0	95.0	100.0	50.0	-	100.0
A. intermedium	100.0	98.9	0.0	21.2	12.5	0.0
A. trichophorum	100.0	88.7	98.8	87.0	31.1	-
Percentage survival						
A. smithii	56.4	89.4	100.0	78.5	-	100.0
A. intermedium	91.7	64.5	0.0	71.4	60.0	0.0
A. trichophorum	100.0	83.3	69.8	79.1	100.0	-
Percentage of plants from seeds						
A. smithii	56.4	82.0	100.0	39.2	-	100.0
A. intermedium	91.7	62.5	0.0	15.2	8.1	0.0
A. trichophorum	100.0	30.6	67.9	64.9	31.1	-

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Folded copies of Bridges' map, on lighter paper	.35
Hughes' map of Salivary Chromosomes of *Drosophila Virilis* (9½ by 18)	.75
Dobzhansky's map of Salivary Chromosomes of *Drosophila Azteca* (9½ by 18)	.75
1 copy each of Painter's Hughes' Dobzhansky's, and Bridges' two maps (5 maps in all)	3.00

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Set of 15 Lantern Slides		9.50
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† Volume and page number of illustration in the JOURNAL OF HEREDITY.

ILLUSTRATED LITERATURE

"Symposium Reprint" on Salivary Gland Chromosomes, containing articles from the JOURNAL OF HEREDITY, 1934-1938, by Painter, Bridges, Metz, Mackensen and Hughes—four Salivary Gland Chromosome maps, 15 illustrations, 54 pages $3.00

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